

Taxonomic and Functional Implications of Mandibular Scaling in Early Hominins

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ABSTRACT Body mass estimates for fossil hominin taxa can be obtained from suitable postcranial and cranial variables. However, the nature of the taphonomic processes that winnow the mammalian fossil record are such that these data are usually only available for the minority of the specimens that comprise the hypodigm of a species.

This study has investigated the link between species mean body mass and the height and width of the mandibular corpus in a core sample of 23 species of extant simians. The slopes of the least-squares regressions for the whole sample and for the hominoid subset are similar. However, the intercepts differ so that for a given body mass, a hominoid will generally have a smaller mandible than a generalized simian.

The same mandibular measurements were taken on 75 early hominin mandibles assigned to eight species groups. When mandibular corpus height- and width-derived estimates of body mass for the fossil taxa were compared with available postcranial and cranial-derived body mass estimates, the eight early hominin species sort into four groups.

The first, which includes *A. afarensis* and *A. africanus*, has mandibles which follow a “generalized simian” scaling relationship. The second group, which comprises the two “robust” australopithecine species, *P. boisei* and *P. robustus*, has mandibles which scale with body mass as if they are “super-simians,” for they have substantially larger mandibles than a simian with the same body mass. The two “early *Homo*” species, *H. habilis sensu stricto* and *H. rudolfensis*, make up the third group. It has mandibular scaling relationships that are intermediate between that of the comparative simian sample and that of the hominoid subsample. The last of the four groups comprises *H. ergaster* and *H. erectus*; their mandibles scale with body mass as if they were hominoids, so that of the four groups they have the smallest mandibles per unit body mass.

These results are related to comparable information about relative tooth size. Their relevance for attempts to interpret the dietary adaptations of early hominins are explored. *Am J Phys Anthropol* 105:523–538, 1998.

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The majority of attempts to predict the body mass of early hominin¹ species have utilized evidence from the postcranial skeleton (McHenry, 1974, 1994; Steudel, 1980;

¹We are persuaded that Hominidae and, thus, hominid are terms best reserved for the African ape clade.

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Jungers, 1988). However, there is a dearth of specimens in which taxonomically valent cranial remains are securely associated with postcranial material that can furnish reliable estimates of body mass. Thus, it is necessary to seek out alternative strategies for recovering information about the body mass of extinct hominins.

In an earlier study the present authors investigated the utility of a range of cranial variables as surrogates for body mass (Aiello and Wood, 1994). When criteria such as standard error of the estimate and percentage prediction error were used to compare cranially derived estimates of body mass with the body masses predicted from postcranial specimens from the same taxa, orbital height, computed orbital area and, to a lesser extent, biporionic width, were found to be as successful at predicting body mass as the best postcranial variables (Aiello and Wood, 1994). A subsequent study used measured orbital area to predict body mass and concluded that this variable was superior to orbital height for this purpose (Kappelman, 1996).

While the use of orbital variables as body mass estimators goes some way to solving the problem of how to link such estimates to particular early hominin taxa, it is still a method that can only be applied to a small proportion of the fossil evidence. For example, among the 129 cranial remains from Koobi Fora included in Wood (1991) orbital height can be used to derive body mass estimates in only 6% of the specimens. Such a small sample in relation to the number of species which are likely to be represented in the Koobi Fora collection (Wood, 1991) means that while it may be possible to use orbital dimensions to derive species estimates of body mass for some early hominin taxa, unless many more well-preserved crania are recovered it will not be possible to use this evidence to derive reliable information about the nature of intraspecific variation in body mass.

The only region of the skull that is preserved in numbers sufficient to provide such evidence is the mandible. For example, mandibles, of varying degrees of completeness, form approximately 40% of the Koobi Fora hominin cranial sample referred to above. We acknowledge that in terms of its effectiveness for estimating body mass, information

from the mandible may not match that from the best of the postcranial and cranial variables, but the exigencies of the hominin fossil record mean that one may not always have access to sufficient numbers of specimens which preserve the variables that perform best in an interspecific context (Smith, 1993; Ravosa, 1996).

In this study we investigate the utility of the mandible for both the prediction of body mass, and for any functional, or any other, insights that may flow from analyzing the relative size of the mandible in early hominin taxa. This investigation addresses the following questions. Is there a consistent relationship between mandible size and body mass within simians, or in a hominoid subsample thereof? If so, do the early hominin species samples scale as simians, or hominoids, or do they have a scaling relationship that is not represented among the extant sample? Can the nature of any departure from the extant models help in attempts to reconstruct the function of the extinct forms? Do the early hominin species that are judged to be megadont also have relatively large mandibles? Finally, if body mass can be recovered from the early hominin mandibular evidence, can such estimates be used to test postulated associations between crania and mandibles?

MATERIALS AND METHODS

The extant sample comprises 250 simian primates (125 females; 125 males) representing 23 species (Table 1). All 23 species were used to calculate the simian regressions; the hominoid regressions were based on a subset of six species. All non-human primates are from the collections of the Natural History Museum, London. The *Homo sapiens* specimens were taken from the Dart collection, University of the Witwatersrand.

Seventy-four mandibles formed the early hominin data set (Table 2). These were drawn from eight species representing three genera. The species are those that are described and used in Wood (1991, 1992a,b). Postcranially derived body mass estimates for the fossil taxa were taken from McHenry (1992, 1994; Ruff et al., 1997) and the body mass estimates based on cranial evidence are those given in Aiello and Wood (1994).

TABLE 1. The sample used in the regression analyses

	Genus	Species	Mass (g)	
			Female	Male
Callitrichidae	<i>Callithrix</i>	<i>jacchus</i>	290 (5)	310 (5)
Cebidae	<i>Alouatta</i>	<i>seniculus</i>	6,400 (6)	8,100 (5)
	<i>Cebus</i>	<i>apella</i>	2,100 (5)	2,860 (5)
Cercopithecinae	<i>Saimiri</i>	<i>sciureus</i>	580 (5)	750 (5)
	<i>Cercocebus</i>	<i>albigena</i>	6,400 (5)	9,000 (5)
	<i>Cercocebus</i>	<i>torquatus</i>	5,500 (5)	8,000 (5)
	<i>Cercopithecus</i>	<i>mitis</i>	4,400 (5)	7,600 (5)
	<i>Cercopithecus</i>	<i>mona</i>	2,500 (5)	4,400 (5)
	<i>Macaca</i>	<i>arctoides</i>	8,000 (5)	9,200 (5)
	<i>Macaca</i>	<i>mulatta</i>	3,000 (5)	6,200 (5)
	<i>Mandrillus</i>	<i>leucophaeus</i>	10,000 (6)	17,000 (5)
	<i>Miopithecus</i>	<i>talapoin</i>	1,100 (5)	1,400 (5)
	<i>Papio</i>	<i>anubis</i>	12,000 (6)	21,000 (5)
	<i>Papio</i>	<i>cynocephalus</i>	15,000 (5)	20,000 (7)
	<i>Colobus</i>	<i>badius</i>	5,800 (5)	10,500 (5)
Colobinae	<i>Presbytis</i>	<i>melalophus</i>	6,600 (5)	6,700 (5)
	<i>Presbytis</i>	<i>obscura</i>	6,500 (5)	8,300 (5)
Hominoidea	<i>Gorilla</i>	<i>gorilla</i>	93,000 (5)	160,000 (5)
	<i>Hylobates</i>	<i>lar</i>	5,300 (5)	5,700 (5)
	<i>Hylobates</i>	<i>syndactylus</i>	10,600 (5)	10,900 (5)
	<i>Pan</i>	<i>trogodytes</i>	31,100 (5)	41,600 (6)
	<i>Pongo</i>	<i>pygmaeus</i>	37,000 (5)	69,000 (5)
	<i>Homo</i>	<i>sapiens</i>	46,330 (12)	51,980 (12)

Figures in parentheses denote the sample sizes. "Simian" regressions are calculated using all taxa. "Hominoid" regressions are based on data from the six species in Hominoidea.

Measurement selection was pragmatic and was based upon which variables could be obtained for the largest sample of fossil hominin mandibles. Two variables were chosen, namely the height and width of the mandible at the midpoint of the first molar (Fig. 1); details of how the measurements are defined and taken are set out in Wood (1991). Other cranial and postcranial data referred to in the paper are taken from Aiello and Wood (1994) and that paper should be consulted for definitions of the variables and for details of the measurement techniques.

Regression lines were fitted to the logarithmically transformed (to base 10) data using the least-squares (LSR), major axis (MA) and reduced major axis (RMA) methods. The arguments for using LSR as the preferred line-fitting method are set out in Aiello and Wood (1994). Two regressions were calculated for the comparative data, one for the full complement of 23 simian species groups and the other for the subsample of six hominoid species.

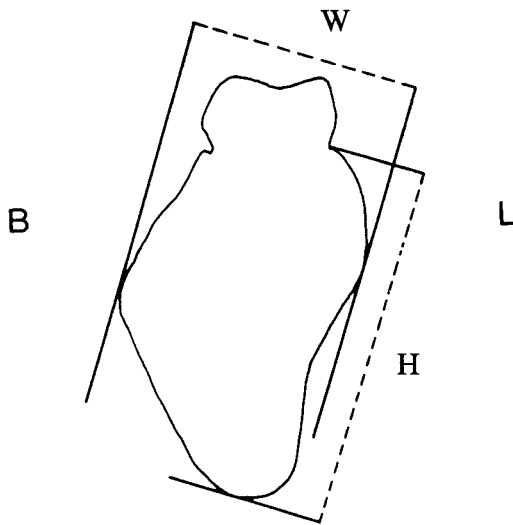
RESULTS

The slopes of the least-squares regressions for mandible height and width are similar in both the pooled-simian and the

TABLE 2. List of the specimens in each of the eight fossil hominin species samples

<i>Australopithecus afarensis</i>	AL 145-35, AL 198-1, AL 207-13, AL 266-1, AL 277-1, AL 288-II, AL 333w-12, AL 333w-32+60, AL 333w-1a+b, AL 400-1a, AL 417-1a, AL 444-2b, LH4
<i>Australopithecus africanus</i>	MLD 18, MLD 34, MLD 40, STS52
<i>Paranthropus boisei</i>	KNM-ER 403, KNM-ER 725, KNM-ER 726, KNM-ER 727, KNM-ER 728, KNM-ER 729, KNM-ER 733, KNM-ER 801A, KNM-ER 805A, KNM-ER 818, KNM-ER 810A, KNM-ER 1468, KNM-ER 1469, KNM-ER 1803, KNM-ER 1806, KNM-ER 3229, KNM-ER 3230, KNM-ER 3729, KNM-ER 3731, KNM-ER 5429, KNM-ER 5877, OMO L74A-21, OMO L7A-125, OMO 18-18, OMO L860-2, PENINJ
<i>Paranthropus robustus</i>	SK 6, SK 12, SK 23, SK 34, TM 1517
<i>Homo habilis sensu stricto</i>	KNM-ER 1501, KNM-ER 1502, KNM-ER 1805, OH 13, OH 37
<i>Homo rudolfensis</i>	KNM-ER 819, KNM-ER 1482, KNM-ER 1483, KNM-ER 1506, KNM-ER 1801, KNM-ER 1802
<i>Homo ergaster/erectus</i> ¹	BK 67, BK 8518, KNM-ER 730, KNM-ER 731, KNM-ER 992, OH 22, OH 23
<i>Homo erectus</i> (late)	ARAGO II, ARAGO XIII, SANGIRAN 1b, SANGIRAN 5, SANGIRAN 8, SANGIRAN 9, TIGENHIF 1, TIGENHIF 2, TIGENHIF 3

¹ Late African *Homo erectus*.



$$\text{AREA} = \pi (H/2).(W/2)$$

Fig. 1. Diagram showing the termini for mandible height and width measurements, together with the formula used to compute the cross-sectional area of the corpus. B = buccal; L = lingual; H = height; W = width.

hominoid-only analyses (Table 3; Fig. 2a,b). The differences between the intercepts are such that for the same body mass a generalized simian will usually have a larger mandible than the equivalent-sized small-bodied hominoid (Figs. 2 and 3). At least two caveats must accompany this "conclusion." First, there are no non-hominoid simians which match the mass of the larger-bodied hominoids (Fig. 2). However, what is evident from that figure is that when hominoid and non-hominoid simian taxa have similar-sized mandibles, the hominoid taxon is more likely to have a larger body mass than its non-hominoid simian equivalent. This difference is evident whichever regression method is used. Second, the slope of the hominoid regression may be unduly influenced by there only being two size categories of extant hominoids.

Which of the two mandibular variables, height or width, should be used for body mass estimation? In general when the performance of the two variables is compared empirically by generating estimates for the body mass of the early hominins, and then

by comparing these estimates with body masses predicted from the postcranial evidence, the estimates based on mandibular height are always closer to the body masses based on the postcranial measurements (Table 4). In contrast, the mandibular width-based estimates are always unrealistically large. Thus, despite its generally lower correlation coefficients (Table 3), mandibular height will be used to generate the body mass estimates based on the fossil hominin mandibles, while the mandibular width data will be referred to when considering the functional implications of any hominin scaling relationships that depart from those observed in the extant samples.

The mandible height-derived estimates of body mass for the individual specimens within each of the hominin species are listed in Table 5. The RMA-predicted body masses are generally slightly larger for all but the very smallest hominin individual in the sample. However, the RMA values are so close to the LSR-predicted body masses that it is not necessary to list them separately. The LSR-predicted body masses are also represented in a series of figures each of which follows a similar format (Figs. 3–6). In each figure two sets of estimates are shown. On the left, as open rectangles, are the body mass estimates generated from the total-sample simian regression equation for each of the mandibles in that species sample. On the right, as solid rectangles, are the body mass estimates for each hominin mandible generated from the hominoid-only regression calculations. The two estimates of body mass for each of the fossil hominin mandibles are listed, by taxon, in Table 5.

In all but one of the figures showing data for the early hominin taxa the dashed horizontal lines are the upper and the lower limits of the range of body mass estimates which are based on non-mandibular evidence. The majority are based on predictions made on the basis of postcranial remains (McHenry, 1992, 1994; Ruff et al., 1997); where other evidence has been used this is indicated in the figure legend. For some species there are sufficient data to justify the calculation of separate estimates for males and females and where these are available they are shown as, respectively, the upper and lower solid horizontal lines.

TABLE 3. Simian-based and hominoid-based regression statistics for mandible height (H_{MAN}) and mandible width (W_{MAN})

Variable	r	N	Least squares regression						Major axis		Reduced major axis	
			Slope	Intercept	See	QMLE	SE	RE	Slope	Intercept	Slope	Intercept
Simian regression equations												
H _{MAN}	0.91	46	2.57	0.63	0.25	1.18	1.17	0.98	3.05	0.02	2.83	0.30
W _{MAN}	0.95	46	2.61	1.57	0.19	1.10	1.09	1.08	2.87	1.34	2.76	1.45
Hominoid regression equations												
H _{MAN}	0.96	12	2.67	0.78	0.14	1.05	1.04	1.05	2.87	0.50	2.78	0.62
W _{MAN}	0.98	12	2.55	1.79	0.11	1.03	1.03	1.07	2.66	1.67	2.61	1.72

Body mass in grams and linear measurements in millimeters. r = product moment correlation coefficient; N = sample size of sex/species points; See = standard error of the estimate; the quasimaximum likelihood estimator (QMLE) = $\exp(s^2/2)$ where s^2 = residual mean square of the regression equation; Smearing estimate (SE) = $1/n \exp(\log r_i)$ where n is the number of cases and $\log r_i$ is the residual of each point in log units; Ratio estimate (RE) = y_i/z_i where y_i is the observed value of the dependent variable Y for the i th observation on the original measurement scale and z_i is the predicted value for the i th observation, detransformed back to the original measurement scale without correction; major axis statistics are included with the least squares regression and reduced major axis-based statistics for comparison.

The eight hominin species form four groups with respect to the way that the mandibles scale in relation to predicted body mass. The first includes the two *Australopithecus* species, *A. afarensis* and *A. africanus*, with both fossil species scaling (Fig. 3) as if they were generalized simians (H_s in Fig. 7). The second group comprises the two *Paranthropus* species, *P. robustus* and *P. boisei*. Both scale as if they are "super-simians" (Fig. 4). That is, they have a substantially larger mandible for their body mass than would be the case for a simian species of the same body mass (H_{ss} in Fig. 7). To put the relationship between body mass and mandibular corpus height of *P. boisei* into context, the species mean body mass estimated on the basis of mandibular height, using the hominoid regression, is more than three times larger than the postcranially based body estimate of body mass (Table 4).

The third group comprises two of the early *Homo* species, *H. habilis sensu stricto* and *H. rudolfensis*. However, it should be noted that in the case of the latter species the only reliable body mass estimates are from cranial evidence, for there are no postcranial specimens which can be reliably associated with *H. rudolfensis* (see below). In both of these early *Homo* species (Fig. 5) the mandibles attributed to them scale between the generalized simian and the hominoid-subset regression values so that individuals belonging to the two species would have a mandible smaller than that of an equivalent-sized generalized simian, but larger than that of an equivalent-sized hominoid. The fourth and last group comprises the man-

dibles attributed to *Homo ergaster* and to late *Homo erectus*. Estimates based on mandibles attributed to *H. ergaster*/early African *H. erectus* specimens and those for the late *H. erectus* sample are given in Figure 6. Both groups scale as if they are hominoids.

DISCUSSION

The mandible is self-evidently an important component of the mammalian, and thus the primate, masticatory system. It functions as a beam and/or lever which converts activity in the muscles of mastication into bite forces. There is abundant evidence that the shapes of the tooth crowns are critical for determining how such bite forces are converted into an efficient system for breaking down food (Kay, 1975; Lucas and Luke, 1984; Maier, 1984; Spears and Crompton, 1994, 1996). Likewise, a series of studies have indicated how the size and the shape of the mandible can also provide important insights into the masticatory function of living and fossil primates (Du Brul, 1977; Smith, 1978, 1983; Hylander, 1979, 1985; Bouvier, 1986; Daegling and Grine, 1991; Schwartz and Conroy, 1996).

The relationship between mandible size and body mass was investigated across a mixed platyrrhine and catarrhine sample of anthropoids by Smith (1983). He eliminated the effects of sexual dimorphism by using female-only samples and showed that there was a strong relationship (e.g. $r^2 = 0.8$) between both the height and width of the mandibular body and body mass. He also showed that the relationships were approximately isometric, but because the slope val-

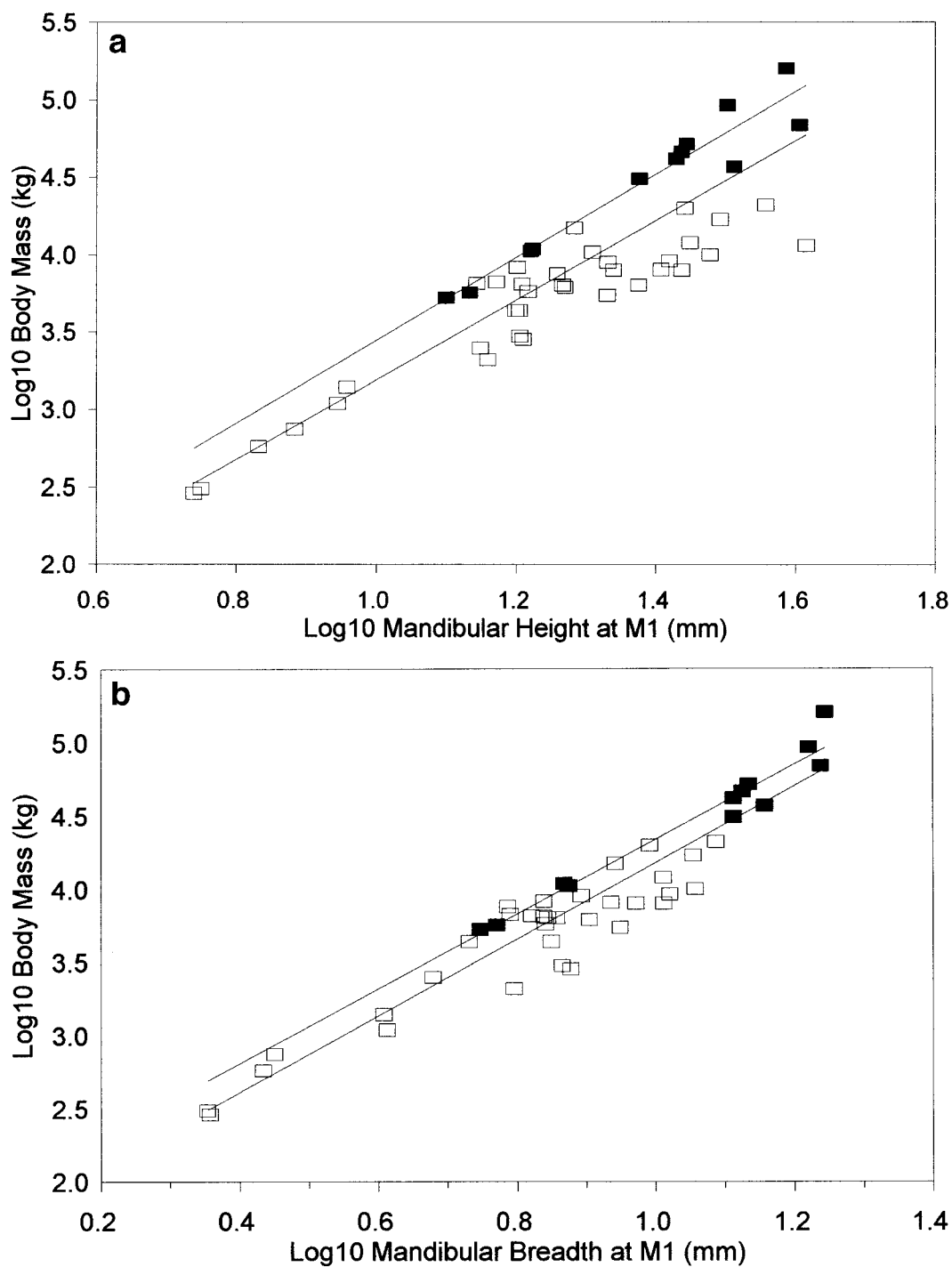


Fig. 2. Plots of (a) \log_{10} mandibular body height at M_1 and \log_{10} body mass and of (b) \log_{10} mandibular body width at M_1 and \log_{10} body mass for the males and females of the whole sample and for the hominoid subsample. Hominoid sample = solid rectangles; simian sample = both solid and open rectangles. Regression statistics are given in Table 3.

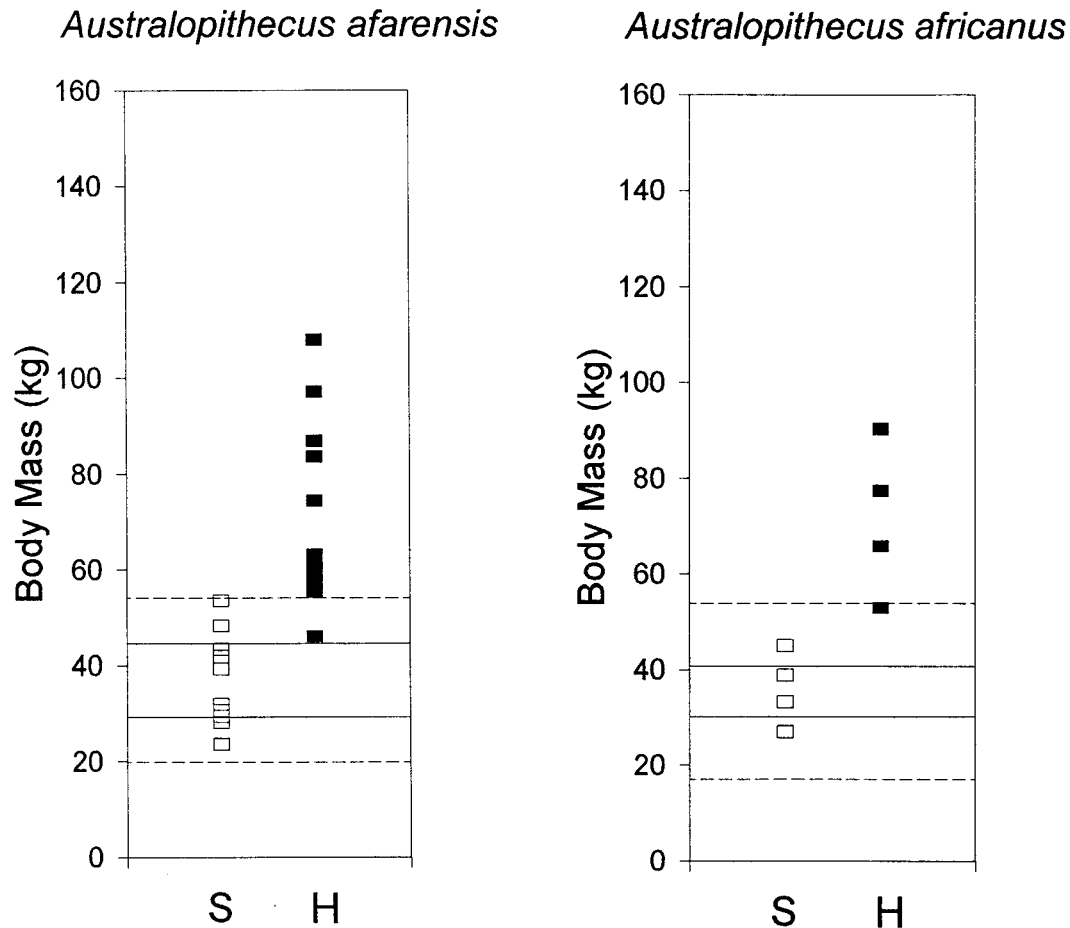


Fig. 3. Body mass estimates for *A. afarensis* and *A. africanus* based on simian and hominoid least squares regressions (S = simian; H = hominoid). In each figure two sets of estimates are shown. On the left, represented as open rectangles, are the body mass estimates for each hominin mandible generated using the total-sample "simian" regression equation. On the right-hand side of each figure, represented as solid rectangles, are the body mass estimates generated from the hominoid-only regres-

sion calculations. The upper solid line in each figure represents the mean postcranially determined body mass for males and the lower, the mean postcranially determined body mass for females. The dashed lines represent the 95% confidence limits for the mean species postcranially determined body mass (McHenry, 1994). The predicted body masses used in this, and subsequent, figures are given in Table 5.

ues for mandibular width were always more positive than those for mandibular height, the larger-bodied species tended to have more robust (i.e. relatively wider) mandibles. This did not seem to be diet-related, for when the taxa were divided into folivore and frugivore subsets, the link with body mass persisted. However, Hylander (1988) makes the point that this may be in large part due to the inclusion of "thin-bodied" platyrrhine mandibles in the sample. When Hylander (1988) reanalyzed a female catarrhine subset of the Smith (1983) data set

the RMA slope was close to unity: i.e., large mandibles were not relatively wider-bodied.

A subsequent study by Bouvier (1986) investigated the relationship between mandibular corpus height and width in male-only samples of 14 species of Cercopithecoidea. There was a similarly strong relationship with body mass (e.g. $r^2 = 0.8$) but in this study, contra the experience of Smith (1983) with the females, there was a tendency for the larger species to have relatively taller mandibular bodies.

TABLE 4. Predicted hominin species body masses based on mandible height and width compared with estimates based on postcranial variables¹

	N	Predicted body mass based on:				Post-crania
		Mandible height		Mandible width		
		Simian-based	Hominoid-based	Simian-based	Hominoid-based	
<i>Australo-pithecus</i>						
<i>afarensis</i>	13/11	38.0 (28.7–50.3)	75.8 (60.8–94.7)	91.5 (69.1–121.4)	121.0 (96.1–152.5)	37.0 (19.9–54.1)
<i>africanus</i>	4/4	36.1 (27.5–47.5)	71.9 (58.4–88.7)	133.3 (97.4–182.7)	174.6 (132.4–230.4)	35.5 (17.1–53.9)
<i>Paranthropus</i>						
<i>robustus</i>	5/5	55.3 (40.1–76.2)	111.9 (85.0–147.5)	196.3 (137.8–280.0)	254.3 (182.4–355.5)	36.1 (17.4–54.8)
<i>boisei</i>	26/26	67.5 (47.7–95.5)	137.9 (100.8–189.0)	264.8 (180.6–388.8)	340.4 (234.4–495.7)	44.3 (20.1–68.5)
<i>Homo</i>						
<i>habilis sensu stricto</i>	5/4	26.3 (20.7–33.5)	51.7 (43.8–61.1)	86.2 (65.5–113.5)	114.1 (91.5–142.5)	34.3 (31.5, 37.0) ³
<i>rudolfensis</i>	6/5	44.5 (33.1–59.8)	89.3 (70.2–113.8)	157.5 (113.0–220.0)	205.2 (151.8–278.0)	55.2 (50.8, 59.6) ³
<i>ergaster/erectus</i> ²	7/7	30.5 (23.7–39.4)	60.4 (50.2–72.7)	99.3 (74.6–132.2)	131.0 (103.3–166.2)	57.5 (52.0, 63.0) ³
<i>erectus</i> (late)	9/9	43.2 (32.3–57.9)	86.6 (68.5–109.6)	94.2 (70.9–125.3)	124.4 (98.5–157.5)	70.6 (58.3–86.7) ⁴

¹ Postcranial species body masses from McHenry (1994) unless otherwise indicated. N = sample size, numbers to the left of the slash refer to samples sizes for the mandibular height analyses and numbers to the right of the slash refer to sample sizes for the mandibular width analyses. Numbers in parentheses are the 95% confidence limits for the predicted body masses. Unless otherwise indicated they are the average confidence intervals of all individual predictions that go into deriving each body weight estimate.

² Late African *Homo erectus*.

³ The smaller mass in parentheses represents the inferred mass for females and the larger for males (McHenry, 1994).

⁴ Masses represent the mean range of inferred masses for five late *H. erectus* individuals (Boxgrove 1, Zhoukoudian FemV, Arago 44, KNM-BK 66, OH28) (Ruff et al., 1997).

The present study deliberately used samples from both the males and females of each species so that the results could be applied to fossils whose sex was unknown. Like its predecessors this analysis also demonstrates a strong correlation between the size of the mandibular corpus and body mass. This is evident in both the total-sample simian regressions and for the regressions based on the hominoid-only subset of the data (Table 3, Fig. 2), and it is these relationships that form the basis of the subsequent analysis of mandibular scaling in the various fossil hominin taxa.

The interpretation of the mandibular scaling evidence within each of the early hominin species samples must be moderated according to how reliable the postcranially derived body mass estimates are judged to be. For example in the case of *A. afarensis*, if we accept that the hypodigm attributed to that taxon does belong to a single, sexually dimorphic species (Richmond and Jungers, 1995; Lockwood et al., 1996; but see Häusler and Schmid, 1995), then the postcranially based body mass estimates are reasonably reliable. Likewise, if the taxonomic unity of the *A. africanus* hypodigm is accepted (but see Clarke, 1988, and Kimbel and White,

1988), then there are several postcranial specimens which provide body mass estimates. Thus the interpretation that, with respect to mandible size, the two australopithecine species scale as generalized simians is a relatively robust one.

When one turns to the evidence about *Paranthropus* there are both actual and potential problems related to the nature of the postcranial evidence linked to the two species samples. In the case of *P. robustus*, which is largely a “single-site” (i.e. Members 1 and 2 at Swartkrans) hypodigm, the debate revolves around the relative likelihood that the limb bones belong to the “majority” or to the “minority” hominin in terms of representation among the dental and gnathic remains (Susman, 1988). Nonetheless, given the considerable preponderance of *P. robustus*-like cranial evidence, it is highly probable that the postcranial evidence belongs to the same taxon.

In contrast, the probability is appreciably lower than the postcranial remains used for the body mass estimations for the second of the two *Paranthropus* species, *P. boisei*, are correctly attributed. The only potential *P. boisei* associated skeleton, KNM-ER 1500, is linked to that taxon on the basis of a frag-

TABLE 5. Mean and 95% confidence limits of the body mass predicted from mandibular height for each of the individuals within the hominin species group

	H_{MAN}^3	Predicted body mass (kg)					
		S_{PBM}^1			H_{PBM}^2		
		Mass	Conf.	Limits	Mass	Conf.	Limits
<i>Australopithecus afarensis</i>							
AL 145-35	28.0	23.7	18.9	29.7	46.3	39.8	53.9
AL 288-li	30.0	28.3	22.1	36.1	55.7	46.9	66.1
AL 333w-12	30.5	29.5	23.0	37.8	58.2	48.8	69.4
AL 266-1	30.5	29.5	23.0	37.8	58.2	48.8	69.4
AL 207-13	30.5	29.5	23.0	37.8	58.2	48.8	69.4
AL 198-1	31.0	30.8	23.9	39.6	60.8	50.6	72.9
LH 4	31.5	32.0	24.8	41.5	63.4	52.6	76.5
AL 417-1a	34.0	39.0	29.5	51.5	77.8	62.7	96.5
AL 333w-1a+b	35.0	42.0	31.5	55.9	84.0	66.9	105.5
AL 400-1a	35.5	43.6	32.6	58.3	87.3	69.1	110.2
AL 277-1	37.0	48.4	35.8	65.6	97.5	75.9	125.2
AL 333w-32+60	38.5	53.6	39.2	73.5	108.4	83.0	141.6
AL 444-2b	41.2	63.8	45.6	89.3	130.0	96.6	174.8
<i>Australopithecus africanus</i>							
STS 52	29.5	27.1	21.3	34.4	53.2	45.1	62.8
MLD 34	32.0	33.4	25.7	43.3	66.1	54.5	80.2
MLD 18	34.0	39.0	29.5	51.5	77.8	62.7	96.5
MLD 40	36.0	45.1	33.6	60.6	90.6	71.4	115.1
<i>Paranthropus boisei</i>							
KNM-ER 3731	30.0	28.3	22.1	36.1	55.7	46.9	66.1
KNM-ER 727	35.0	42.0	31.5	55.9	84.0	66.9	105.5
OMO 18-18	35.0	42.0	31.5	55.9	84.0	66.9	105.5
OMO L860-2	35.5	43.6	32.6	58.3	87.3	69.1	110.2
KNM-ER 728	37.0	48.4	35.8	65.6	97.5	75.9	125.2
KNM-ER 3729	38.0	51.9	38.0	70.8	104.7	80.6	136.0
KNM-ER 3229	39.0	55.4	40.3	76.2	112.2	85.5	147.4
KNM-ER 733	39.5	57.3	41.5	79.1	116.1	87.9	153.3
PENINJ	40.0	59.2	42.7	82.0	120.1	90.4	159.5
KNM-ER 810A	40.0	59.2	42.7	82.0	120.1	90.4	159.5
KNM-ER 725	41.0	63.0	45.2	88.0	128.3	95.6	172.2
KNM-ER 805A	41.0	63.0	45.2	88.0	128.3	95.6	172.2
KNM-ER 3230	42.0	67.1	47.7	94.3	136.8	100.8	185.6
KNM-ER 1803	42.0	67.1	47.7	94.3	136.8	100.8	185.6
KNM-ER 801A	43.5	73.4	51.6	104.4	150.3	109.0	207.1
OMO L74A-21	43.5	73.4	51.6	104.4	150.3	109.0	207.1
KNM-ER 5429	44.0	75.6	52.9	107.9	154.9	111.8	214.6
KNM-ER 729	44.0	75.6	52.9	107.9	154.9	111.8	214.6
KNM-ER 5877	44.0	75.6	52.9	107.9	154.9	111.8	214.6
KNM-ER 1806	44.5	77.8	54.3	111.4	159.7	114.7	222.3
KNM-ER 1469	46.0	84.7	58.5	122.6	174.5	123.4	246.6
KNM-ER 726	46.0	84.7	58.5	122.6	174.5	123.4	246.6
KNM-ER 403	47.0	89.5	61.4	130.5	184.8	129.5	263.8
KNM-ER 1468	48.0	94.5	64.4	138.6	195.5	135.7	281.7
OMO L7A-125	48.5	97.0	65.9	142.8	201.0	138.8	291.0
KNM-ER 818	50.0	104.9	70.6	156.0	218.0	148.5	320.2
<i>Paranthropus robustus</i>							
TM 1517	35.0	42.0	31.5	55.9	84.0	66.9	105.5
SK 6	37.5	50.1	36.9	68.1	101.1	78.2	130.5
SK 23	38.0	51.9	38.0	70.8	104.7	80.6	136.0
SK 34	40.5	61.1	43.9	85.0	124.1	93.0	165.7
SK 12	43.0	71.2	50.3	101.0	145.7	106.3	199.7
<i>Homo habilis</i>							
KNM-ER 1502	27.0	21.6	17.3	26.9	42.0	36.4	48.5
OH 13	27.5	22.6	18.1	28.3	44.1	38.1	51.1
KNM-ER 1501	29.0	25.9	20.5	32.8	50.8	43.3	59.7
KNM-ER 1805	30.0	28.3	22.1	36.1	55.7	46.9	66.1
OH 37	32.0	33.4	25.7	43.3	66.1	54.5	80.2
<i>Homo rudolfensis</i>							
KNM-ER 1482	31.0	30.8	23.9	39.6	60.8	50.6	72.9
KNM-ER 1506A	33.0	36.1	27.6	47.3	71.8	58.5	88.1
KNM-ER 1801	34.0	39.0	29.5	51.5	77.8	62.7	96.5
KNM-ER 819	38.0	51.9	38.0	70.8	104.7	80.6	136.0
KNM-ER 1802	38.0	51.9	38.0	70.8	104.7	80.6	136.0
KNM-ER 1483	39.5	57.3	41.5	79.1	116.1	87.9	153.3

(continued)

TABLE 5. (continued). Mean and 95% confidence limits of the body mass predicted from mandibular height for each of the individuals within the hominin species group

	H_{MAN}^3	Predicted body mass (kg)					
		S_{PBM}^1			H_{PBM}^2		
		Mass	Conf.	Limits	Mass	Conf.	Limits
<i>Homo ergaster</i> /late African <i>Homo erectus</i>							
KNM-ER 731	27.0	21.6	17.3	26.9	42.0	36.4	48.5
OH 22	28.5	24.8	19.7	31.3	48.5	41.5	56.7
BK 8518	30.0	28.3	22.1	36.1	55.7	46.9	66.1
KNM-ER 992	31.5	32.0	24.8	41.5	63.4	52.6	76.5
KNM-ER 730	31.5	32.0	24.8	41.5	63.4	52.6	76.5
OH 23	33.0	36.1	27.6	47.3	71.8	58.5	88.1
BK 67	34.0	39.0	29.5	51.5	77.8	62.7	96.5
Late <i>Homo erectus</i>							
ARAGO II	30.5	29.5	23.0	37.8	58.2	48.8	69.4
ARAGO XIII	32.5	34.7	26.6	45.3	68.9	56.5	84.1
TIGENHIF 2	35.0	42.0	31.5	55.9	84.0	66.9	105.5
SANGIRAN 8	35.5	43.6	32.6	58.3	87.3	69.1	110.2
SANGIRAN 1b	36.0	45.1	33.6	60.6	90.6	71.4	115.1
SANGIRAN 9	36.0	45.1	33.6	60.6	90.6	71.4	115.1
TIGENHIF 1	36.0	45.1	33.6	60.6	90.6	71.4	115.1
TIGENHIF 3	38.0	51.9	38.0	70.8	104.7	80.6	136.0
SANGIRAN 5	38.0	51.9	38.0	70.8	104.7	80.6	136.0

Within each species the mandibles are listed in ascending order of mandibular height.

¹ S_{PBM} = predicted body mass using the total-sample simian regression.

² H_{PBM} = predicted body mass using the hominoid-only regression.

³ H_{MAN} = mandibular corpus height (mm) at M_1 .

ment of mandibular corpus (Grausz et al., 1988) that one of us has judged to be difficult to assign at the level of the genus (Wood, 1991). However, cranially derived *P. boisei* body mass estimates are available for the type specimen of *P. boisei* (OH 5), and from specimens which are almost certainly, KNM-ER 406, or very likely, KNM-ER 732, to be correctly attributed to that taxon (Aiello and Wood, 1994; Kappelman, 1996). These cranially based estimates suggest that the range of body mass indicated for *P. boisei* by the horizontal dashed lines in Figure 4 is not an unreasonable one. Thus, the interpretation offered for the two *Paranthropus* species, that their mandibles are unusually tall and broad for their body mass (see H_{ss} in Fig. 7), is one to which we can attach a reasonable degree of reliability.

The evidence for the postcranially derived body mass data for *H. habilis sensu stricto* comes from material from Olduvai and Koobi Fora. The difficulty with these sources of data is that at both sites there are alternative hominin taxa to which the specimens could be assigned and any interpretation of the mandibular data should reflect this uncertainty. An even greater degree of skepticism should be associated with the postcrani-

ally derived body masses given for *H. rudolfensis*. The body mass estimates given for *H. rudolfensis* in Figure 5 are from two femoral specimens, KNM-ER 1472 and 1481, that have been cautiously assigned to *H. rudolfensis*. However, the only grounds for allocating these specimens to *H. rudolfensis* are that the material is 1) evidently not australopithecine or paranthropine in its morphology (Wood, 1976; Kennedy, 1983; MacLatchy, 1996), and 2) contemporaneous with the cranial remains that have been assigned to *H. rudolfensis*. The second of the two reasons, the contemporaneity argument, has little force because the postcranial specimens could equally well belong to early African *H. erectus*, the cranial remains of which have been found in equivalent-aged strata (Kennedy, 1983; Wood, 1991). There is only one cranial specimen of *H. rudolfensis*—KNM-ER 1470—for which it is possible to use orbital measurements to estimate the body mass. The 95% CI interval values for the orbital height-predicted body mass are 43–63 kg (Aiello and Wood, 1994). These estimates do not, on the grounds of size incompatibility, preclude the postcranial specimens previously referred to from belonging to *H. rudolfensis*, but neither do

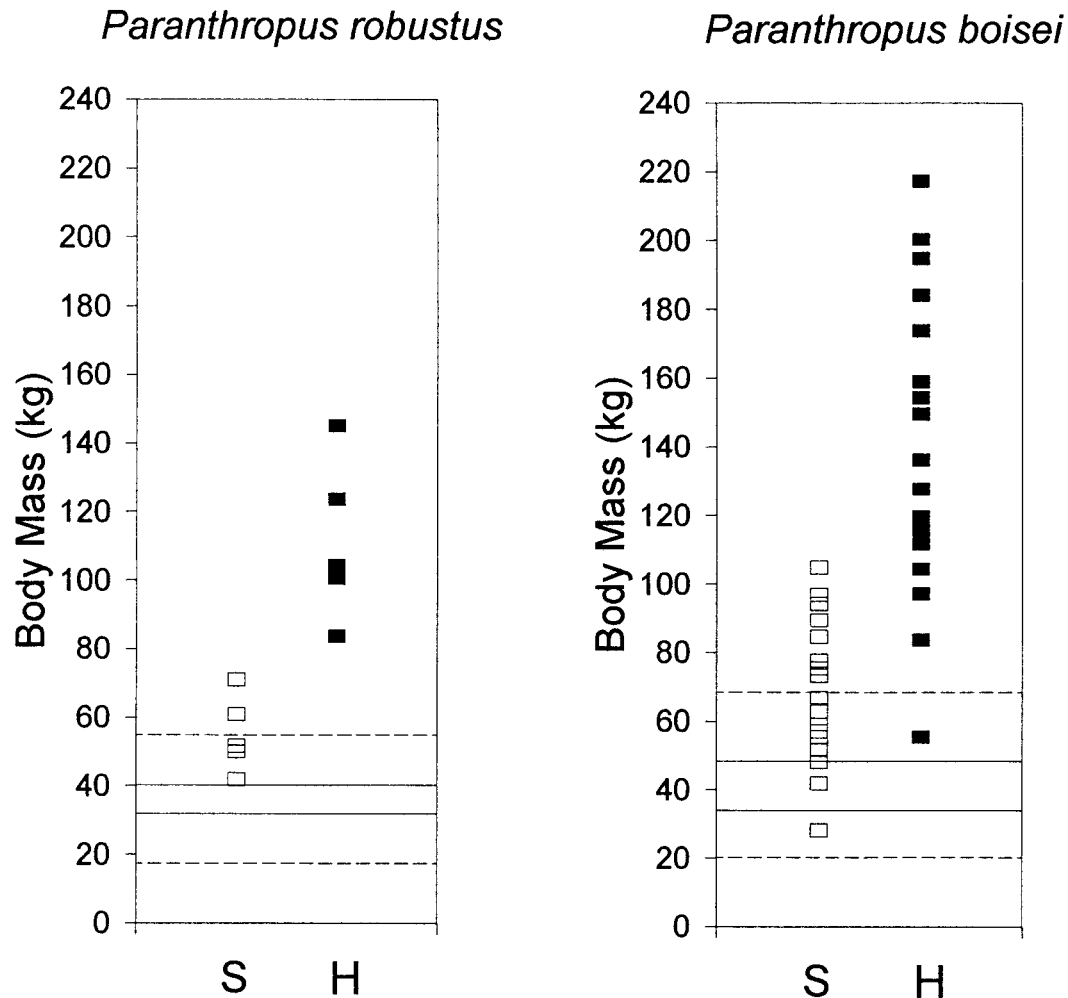


Fig. 4. Body mass estimates for *P. robustus* and *P. boisei* based on simian and hominoid least squares regressions (S = simian; H = hominoid). For an explanation of the conventions used please see the legend for Figure 3.

they provide any strongly positive evidence for linking KNM-ER 1472 and 1481 with *H. rudolfensis*.

The postcranial data that are the basis for the body mass estimates for *H. ergaster*/early African *H. erectus* are as reliable as those for any of the other species considered in this discussion. This is mainly because the securely associated skeleton, KNM-ER 15000, provides particularly compelling evidence of a link between cranial and postcranial morphology. Given the controversy surrounding the boundary between archaic *Homo sapiens* and late *Homo erectus* and the

lack of good, associated, skeletal evidence, the postcranially based body mass estimates given in for late *Homo erectus* in Figure 6 must be regarded as less precise than those for *H. ergaster*/early African *Homo erectus*.

A further general note of caution needs to be recorded in relation to the fossil hominin mandible sample. It concerns the effects on the mandible of post-mortem taphonomic processes. Some mandibles have lost surface bone through weathering and thus the fossils are smaller than the pristine mandible would have been. In others the mandibular body is permeated by many matrix-filled

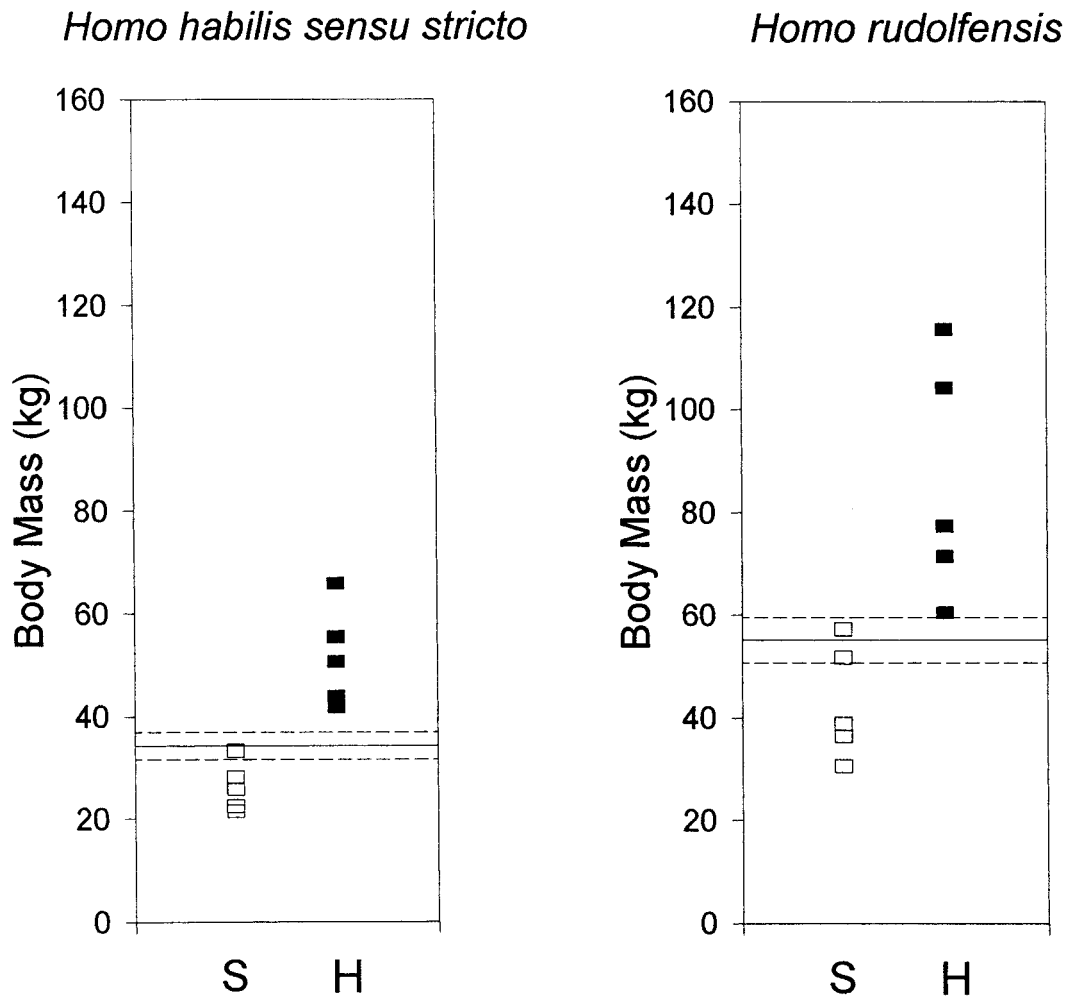


Fig. 5. Body mass estimates for *H. habilis sensu stricto* and *H. rudolfensis* based on simian and hominoid least square regressions (S = simian; H = hominoid). In each figure two sets of estimates are shown. On the left, represented as open rectangles, are the body mass estimates for each hominin mandible generated using the total-sample "simian" regression equation. On the

right-hand side of each figure, represented as solid rectangles, are the body mass estimates generated from the hominoid-only regression calculations. The solid lines represent the species mean body mass. The upper dotted line represents the inferred mean body mass for males and the lower dotted line the inferred mean body mass for females (McHenry, 1994).

cracks which increase the size of the specimen. These effects are common in the *P. boisei* sample (Wood, 1991) and appropriate allowances need to be made especially when interpreting "outlying" specimens.

What are the functional implications of the four different patterns of early hominin mandibular scaling relationships which have been noted in this study? Compared with the living hominoid sub-sample all the australopithecine, "early *Homo*" and paranthropine

hominin species have large, or excessively large, mandibular corpora relative to body mass. One of the first studies to investigate the comparative context and functional implications of the shape of the mandibular corpus of primates (Hylander, 1979) showed that, per unit of mandibular length, the jaws of anthropoids were taller than those of prosimians. This was interpreted as an adaptation to enable anthropoids to "counter internal stress in the mandible due to the

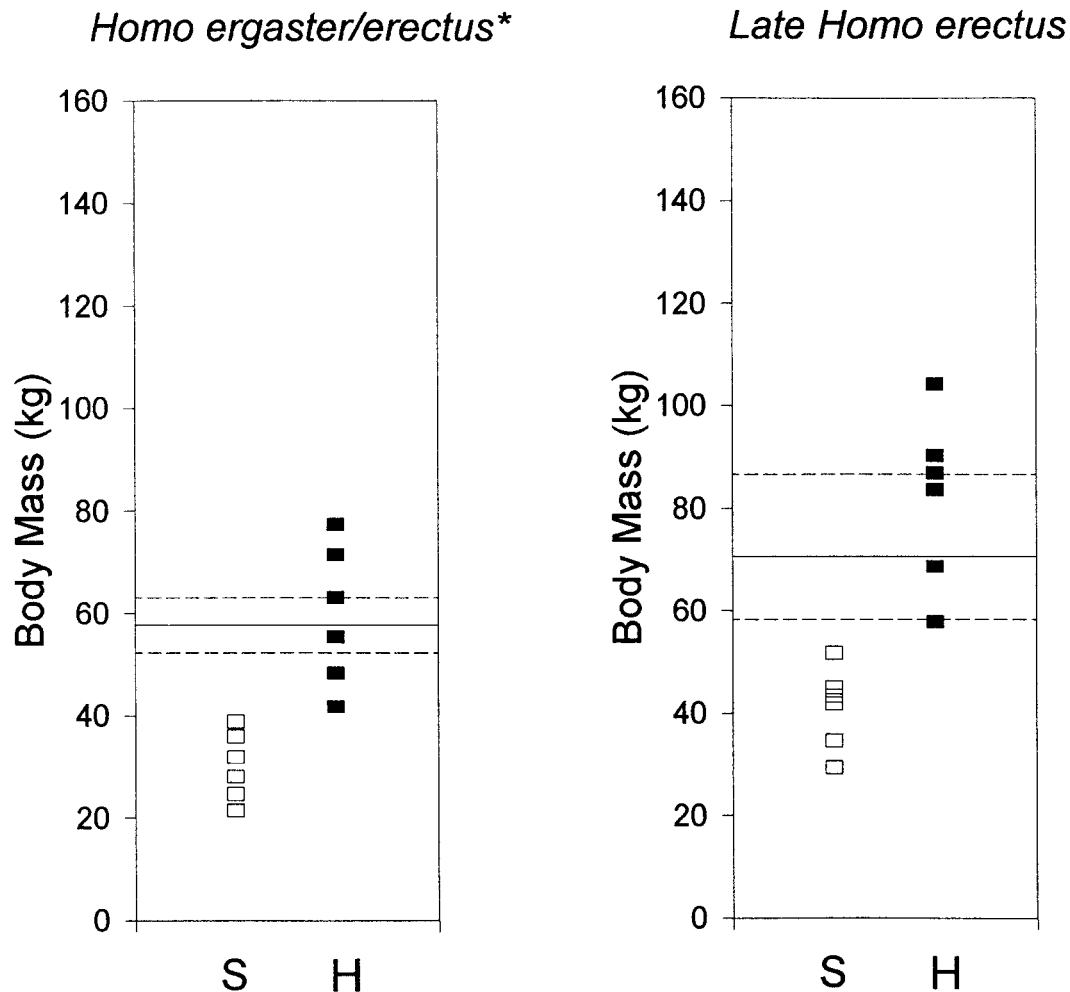


Fig. 6. Body mass estimates for early African *H. erectus*/*H. ergaster* and late *Homo erectus* (*H. erectus sensu stricto*) based on simian and hominoid least squares regressions (S = simian; H = hominoid). In each figure two sets of estimates are shown. On the left, represented as open rectangles, are the body mass estimates for each hominin mandible generated using the total-sample "simian" regression equation. On the right-hand side of each figure, represented as solid rectangles, are the body

mass estimates generated from the hominoid-only regression calculations. For *H. erectus*/*H. ergaster*, the solid and dotted lines are as in Figure 5. For *H. erectus*, the single solid line represents mean body mass based on data for five late *Homo erectus* specimens from Africa, Europe and Asia given in Ruff et al. (1997). Dotted lines represent the range of these body masses. *Early African *Homo erectus*.

increased use of balancing-side musculature during unilateral biting" (Hylander, 1979, p. 228). In the same study it was shown that within the simians, if the length of the tooth row is held constant, then the mandibular bodies of the colobines were found to be taller than those of cercopithecines. The functional explanation put forward in this case was that the taller mandibles of the colobines were "primarily a response to pre-

vent mandibular bone fatigue due to cyclical repetitious bending loads" associated with the mastication of leaves (Hylander, 1979, p. 230).

Smith (1983) examined the relationship between mandible size and shape and body mass in samples of females of 32 species of anthropoids, and Bouvier (1986) investigated the same relationships in male Old World monkeys. In contrast to Hylander

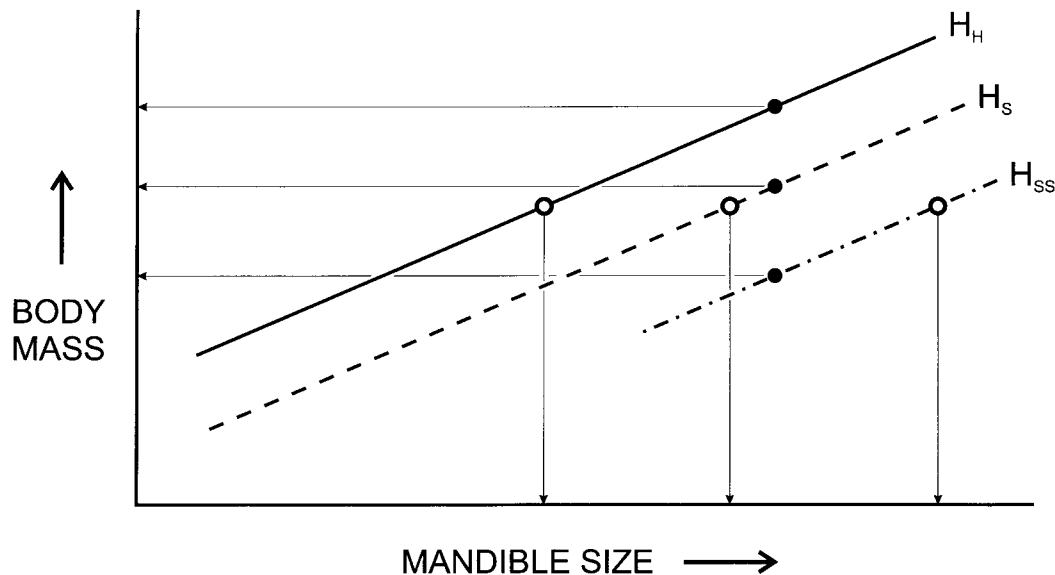


Fig. 7. Simplified diagram of the observed relationship between mandible size and body mass. H_H = hominoid regression line; H_S = simian regression line; H_{SS} = "super" simian regression line. Solid circles indicate the three body mass estimates for a similar-sized mandible; open circles, the size of the mandibles predicted for an animal with the same body size.

(1979), who scaled mandibles against the length of the tooth row, the results of Smith and Bouvier suggest that it is not the colobines but the cercopithecines which have the taller mandibles relative to body mass. Bouvier (1986) attributes this to the "long faces and inefficient masticatory muscle arrangements" in cercopithecines (p. 481). Smith (1983) suggests that a diet that induces excessive twisting of the corpus may be the factor which determines the latter's larger size in cercopithecines, but twisting moments are best countered by increasing the thickness rather than the height of the mandible. If this is also the case within hominins then diet-induced parasagittal bending and torsion (Hylander, 1988), in excess of that seen in hominoids, is greatest in the two paranthropine species and least in *Homo ergaster* and late *H. erectus*. The two australopithecine species are interpreted as having levels of torsion comparable to those in living simians with "early *Homo*" having torsional loads that are intermediate between those of simians and hominoids. Some idea of the scale of this "excess" of mandibular material in *P. boisei* is given by the inference that for an average homi-

noid to have a mandible of the same corpus height it would need to be approximately four times the estimated body mass of its paranthropine equivalent.

These comparisons are all simplistic in that they are predicated on the assumption that the internal structure of the extant and fossil mandibles is comparable and functionally equivalent. As the details of the internal structure of extant (Daegling, 1989) and fossil mandibles (Daegling and Grine, 1991; Schwartz and Conroy, 1996) are progressively explored, and as the analysis of the biomechanical implications of that structure are improved (e.g. Chen and Povirk, 1996), we look forward to more sophisticated interpretations of the functional implications of the differing patterns of early hominin mandibular scaling.

How do these mandibular data relate to information about relative tooth size in early hominin taxa? They are apparently consistent with that evidence (McHenry, 1992; Wood, 1996). The latter study concluded that *H. ergaster* was the only early hominin whose relative tooth size was equivalent to that in modern humans. In the present study *H. ergaster* and late *Homo erectus* are

the only early hominin species whose mandibles are the size that would be predicted if those species were assumed to follow the hominoid scaling regime (see H_H in Fig. 7).

Can these mandibular scaling relationships help in the task of linking cranial with mandibular remains? Although there are strong grounds for linking crania and mandibles when a hominin species is the only one found at a site, for many early hominin species the evidence for associating crania with mandibles is a good deal more tenuous. Examples of this second category of association between cranial and mandibular evidence are the incorporation of crania such as KNM-ER 1470 and the mandibles KNM-ER 1483 and 1802 within the hypodigm of *H. rudolfensis*, and the linking of the cranium KNM-ER 1813 and the mandibles KNM-ER 1501 and 1502 as components of the Koobi Fora hypodigm of *H. habilis sensu stricto*. Does mandibular scaling help by providing body mass estimates which either support or weaken these putative associations? On the face of it the match between the respective body masses predicted from the crania, KNM-ER 1470 and 1813 (Aiello and Wood, 1994), and, respectively, the mandibles, KNM-ER 1802 and 1483 for the former cranium and, the mandibles 1501 and 1502, for the latter (Table 4) (i.e. c. 50–60 kg and c. 20–25 kg) is a good one, but the estimates have such wide confidence intervals (Smith, 1996) that the best that can be claimed is that the proposed combinations of crania and mandibles within the hypodigms of *H. habilis sensu stricto* and *H. rudolfensis* cannot be refuted by the mandible-based body mass estimates generated in this study.

CONCLUSIONS

Evidence from a comparative sample of extant simians shows that there is a relatively strong link between mandibular corpus size and species body mass. This link is sufficiently strong to be able to predict that for a given body mass a simian is likely to have a larger mandibular corpus than an equivalent-sized hominoid.

The mandibular scaling relationships of the eight early hominin species included in this study fall into one of four categories. The two australopithecine species scale as if

they were generalized simians, whereas the two paranthropine taxa, *P. boisei* and *P. robustus*, behave as if they were “super-simians” for their mandibles are substantially larger than those of a simian of the same body mass. The third group comprises the two “early *Homo*” taxa, that is *H. habilis sensu stricto* and *H. rudolfensis*. They both have mandibles that are intermediate between the simians and the hominoids in the way that they scale with body mass. The fourth group, *H. ergaster*/early African *H. erectus* and late *H. erectus*, have mandibular bodies of the size that would be predicted using the hominoid scaling relationship.

This outcome is consistent with what is known about the relative size of the molar tooth crowns, for among the early hominins it is only *H. ergaster* and late *H. erectus* that have modern human-like molar crown size/body mass relationships. All the other early hominin taxa used in this study are “megadont” relative to modern humans. This new mandibular evidence adds further weight to the proposal that there is a significant difference between the masticatory adaptations of the *H. ergaster*/*H. erectus* group and those of all the other early hominin species represented in the study.

The results of the study also confirm that *Paranthropus* apparently displays a masticatory functional complex that has no parallel in the living large-bodied hominoid primates. Any attempts to interpret the diet of *Paranthropus* will need to account for this “extra” mandibular corpus material (e.g., Hylander, 1979, 1988) and integrate these results into a functional scenario that can also “explain” the dental specializations that apparently characterize the “robust” australopithecines.

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